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How will warming affect the salt marsh foundation species *Spartina patens* and its ecological role?

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Abstract Foundation species structure environments and create refuge from environmental stress. In New England high salt marsh, the grass *Spartina patens* is a foundation species that reduces salinity, anoxia, desiccation, and thermal stresses through canopy shading and root proliferation. In a factorial *S. patens*-removal and warming field experiment, foundation species removal strongly impacted every aspect of the community, reiterating the important role of the foundation species *S. patens* in the high marsh. Given this central role, we hypothesized that facilitation by the foundation species would be even more important under warmer conditions by ameliorating more severe thermal stress. However, the ecological role of *S. patens* was unaffected by experimental warming, and, independent of the presence of the foundation species, warming had only weak effects on the salt marsh ecological community. Only the foundation species itself responded strongly to warming, by significantly increasing aboveground production in warmed plots. Apparently, amelioration of thermal stress is not as important for salt marsh ecosystem function as *S. patens*' moderation of salinity and desiccation stresses. From these experimental results, we anticipate that climate change-associated thermal stress will not greatly affect *S. patens*-dominated high marsh communities. In contrast, foundation species loss, an emergent conservation issue in Atlantic salt marshes, represents a critical threat to salt marsh ecosystem function.

Keywords Climate change · Salt marsh die-off · Ecosystem engineer · Epifauna

Introduction

Foundation species (sensu Dayton 1972) promote the development and persistence of ecological communities by modifying the structure and physical conditions of a habitat. Diverse environments, such as kelp forests, mussel beds, temperate forests, and salt marshes, are dominated by one or several foundation species that facilitate other organisms by creating a refuge from predation and/or environmental stress (Altieri et al. 2007; Bruno and Bertness 2001; Dayton 1975; Ellison et al. 2005).

Anthropogenic climate change is altering environmental stress regimes. Projected temperature increases between 1.1 and 6.4°C by 2100 (IPCC 2007) will increase thermal stress in many environments. Some ecological communities, such as tropical insects (Deutsch et al. 2008) and organisms in the high intertidal (Harley 2003; Somero 2005), live on the cusp of their thermal limits and are prone to radical change with small increases in temperature. Scientists predict that the effects of climate change on these sensitive communities will depend on the availability of appropriate microclimates (Kearney et al. 2009), which are often structured by foundation species (Dayton 1972; Jones et al. 1997; Moore et al. 2007).

Facilitative interactions, such as those between foundation species and the ecological community they support, are strongest where environmental and/or predation stress is high (Bertness and Leonard 1997; Bruno et al. 2003; Callaway et al. 2002; Crain 2008; Hacker and Gaines 1997). Therefore, we expect that increases in thermal stress will drive more frequent or stronger facilitation of communities by foundation

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species. This hypothesis is supported by evidence that interactions between foundation species and associated organisms vary over latitudinal gradients in climate and are more positive where thermal stress is high. For example, Leonard (2000) found that the canopy-forming alga *Ascophyllum nodosum* facilitated the survival of rocky intertidal *Semibalanus balanoides* barnacles only in places and years of higher thermal stress. Analogously, in New England salt marshes, high marsh grasses were net facilitators more of the time and for a greater number of associated plant species in warmer southern New England than in cooler northern New England (Bertness and Ewanchuk 2002).

In salt marshes, halophytic grasses are ecosystem engineers (Jones et al. 1997) that trap and bind suspended sediments that build marsh (Redfield 1972). These grasses ameliorate harsh physical stress at the soil surface by limiting temperatures and soil salinities with canopy shading and oxygenating soils with rhizome and root proliferation. The removal of the plant canopy quickly results in hypersaline soils (Bertness 1991a; Bertness and Ewanchuk 2002; Bertness and Hacker 1994; Whitcraft and Levin 2007), nitrogen and oxygen depletion (Bertness 1991b; Brewer and Bertness 1996; Buckeridge and Jefferies 2007), higher understory temperatures (Bertness and Ewanchuk 2002), changes in algal composition, and loss of macrofaunal diversity (Whitcraft and Levin 2007). In New England, the high salt marsh is dominated by a single foundation species, the grass *Spartina patens* (Bertness and Ellison 1987). Removal of the *S. patens* canopy creates hypersaline patches that are inhospitable to seedlings and slow to revegetate (Bertness et al. 1992; Bromberg Gedan et al. 2009; Shumway and Bertness 1992).

We hypothesized that facilitation by the foundation species *S. patens* would be a primary determinant of the salt marsh community response to warming temperatures. Because thermal stress is linked to salinity stress through the evaporation of seawater, we expected that warming would exacerbate thermal and salinity stresses and elicit ecological effects within the community, and that these effects would be stronger when the facilitator *S. patens* was removed, exposing the sub-canopy community to ambient stress. To test this hypothesis, we warmed plots and manipulated the presence of *S. patens* in a factorial field experiment. We examined the response of plants and animals to characterize the ecological response to warming with and without *S. patens*.

Materials and methods

Experimental design

To investigate the effects of warming with and without the foundation species *Spartina patens*, we conducted a factorial field experiment manipulating ambient temperature and vegetation presence in the *S. patens* zone of Nag Creek Marsh on Prudence Island, part of the Narragansett Bay National Estuarine Research Reserve in Rhode Island (41°37.546N, 71°19.223W). The temperatures in Rhode Island [23°C mean and 28.1°C mean daily maximum in July at the T. F. Green Airport weather station, 7.5 km from the field site (National Climatic Data Center 2003)], even augmented by our experimental warming treatment, are not warm enough to chronically stress the foundation species *S. patens*, which like other C_4 grasses is adapted to warm climates (Ehleringer et al. 1997). However, maximum daily temperatures at the field site are high enough to stress the community of invertebrates associated with *S. patens*, whose thermal tolerance and thermal optimum are much lower (Deutsch et al. 2008). Tidal range at the site is 1.3 m, and the *S. patens* zone is inundated approximately 8 times per month by spring tides.

In 2003, we randomly assigned thirty-two 0.5 × 0.5-m plots to one of two vegetation treatments (*Spartina* removal or control) and one of two warming treatments (warming chamber or control) ($n = 8$ per treatment combination). *Spartina*-removal plots were treated with Round-Up systemic herbicide to kill above- and belowground growth (see Bertness 1991a, b). In the spring of 2004, the grass canopy was removed with a weed-whacker and plots were covered with black weed-block cloth during the summer of 2004 to ensure complete plant death. During the experiment in summer 2005, plant recruits were weeded monthly from *Spartina*-removal plots to maintain the treatment.

Warming was achieved with a pentagonal open top chamber made of corrugated LEXAN polycarbonate (1 m diameter, 0.5 m height) that passively focused sunlight and trapped heat to warm the air within the chamber. This design has been used in other short-stature plant communities for moderate increases in mean air (1.0–1.8°C) and soil (0.6–3.0°C) temperatures (Hollister and Webber 2000; Marion et al. 1997). Chambers were placed on plots in early May and removed in October 2005.

Abiotic stress

Both warming and vegetation treatments were expected to alter the abiotic stress regime of the high marsh. We anticipated that thermal, salinity, anoxia, and desiccation stresses could be affected. We measured salinity of soil porewater, extracted from the top 5 cm of soil with a syringe, using a refractometer (Sper Scientific, Scottsdale, AZ). Soil anoxia was indicated by redox potential, measured at the soil surface in relative mV with an Orion redox probe (Thermo Fisher Scientific, Beverly, MA). Desiccation stress was measured with potential evaporation and relative humidity, quantified with water loss from a wetted sponge (see

Bertness et al. 1992 for methods) and with a Kestrel 3000 pocket weather station held 10 cm above the peat surface (Nielsen-Kellerman, Boothwyn, PA), respectively. Edaphic sampling was done on representative hot summer days during neap tides, conditions that intensify high marsh physical stress, to maximize the likelihood of detecting treatment effects. Sampling dates were 2 June (humidity and potential evaporation), 20 June (salinity, humidity, and potential evaporation), 27 June (redox potential), and 6 July (redox potential) in 2005. Prior to analysis, multiple samples from each replicate plot were averaged.

In each plot, we measured air and surface temperatures to quantify the temperature effects of the warming and vegetation treatments. Air and surface temperatures were recorded hourly through the growing season (May–August) with iButton dataloggers (±0.1°C, Maxim/Dallas Semiconductor, Dallas, TX) affixed to a PVC stake at the center of each plot, suspended 10 cm above the soil ("air temperature") and at the soil–air interface ("soil temperature"). For statistical comparisons, we calculated the average hourly air and soil temperatures in each plot.

Ecological response

We evaluated impacts on the ecological community in two ways, primary productivity of algae and vascular plants and epifaunal composition. Treatment effects on these ecological metrics indicate disruption of salt marsh ecosystem functioning.

Microalgal productivity was assayed with chlorophyll a concentration, an aggregate measurement of algae, diatoms, and cyanobacteria. Three soil core sub-samples (2 cm diameter) were taken from each plot on 1 August 2005. The top 5 mm of the cores was separated, freeze dried, and incubated in 90% acetone. Chlorophyll a concentration was measured using a standard acidification spectrophotometric method (Lorenzen 1967). The three plot sub-samples were averaged prior to data analysis. Vascular plant productivity, predominantly that of *S. patens*, was measured in plots where the plant canopy was left intact. Biomass was sampled from a haphazardly placed 10 × 10-cm quadrat within each plot in September after the plants had flowered. Plants were clipped at the soil surface and live and dead biomass were separated, thoroughly dried at 60°C and weighed.

We sampled epifaunal abundance with pit traps. Pit traps were made from 50-ml centrifuge tubes (diameter 2.5 cm) with 1-mm drainage holes in the base. In each plot, traps were placed in core holes flush with the peat surface and emptied weekly over 4 weeks in June and July 2005. Collections were washed over a 1-mm sieve and sorted to species or morphospecies. For data analysis, animals were grouped by taxonomic class to de-emphasize rare species, and an average weekly catch was calculated for each plot.

Statistical analysis

The effects of experimental treatments on edaphic conditions (redox potential, salinity, potential evaporation, humidity, soil temperature, and air temperature) and epifaunal composition (abundance by class) were assessed with separate factorial multivariate ANOVA (MANOVA), with the main effects of warming treatment and vegetation-removal treatment and their interaction as predictor variables. Treatment effects on chlorophyll a concentration were analyzed with a factorial two-way ANOVA of the same structure. The effect of warming on vascular plant productivity, measured only in vegetated plots, was analyzed with a one-way ANOVA. Prior to analysis, the Shapiro–Wilk and Levene's tests were used to verify that all response variables met ANOVA and MANOVA assumptions of normality and homogeneity of variance. Epifaunal abundance within each class had to be $\log_{10}$ transformed to meet assumptions.

A significant interaction term ($P < 0.05$) in MANOVA and ANOVA indicated the response to warming was conditional upon the vegetation treatment, that is, a warming-driven shift in the interaction between the foundation species and the response variable. In the case of a significant effect in MANOVA of treatments on epifaunal composition or edaphic conditions, factorial ANOVAs were used to explore treatment effects within epifaunal classes and single edaphic variables. In the case of significant interactions in factorial ANOVA, Tukey's honest significant difference post hoc tests were used to test for differences between treatment combinations. All analyses were done with JMP statistical software (version 5.0.1.2, SAS Institute).

Results

Abiotic stress

Warming and vegetation removal significantly affected edaphic conditions (MANOVA, vegetation-removal effect, $F_{6,23} = 20.29$, $P < 0.0001$; warming effect, $F_{6,23} = 50.52$, $P < 0.0001$; interaction $F_{6,23} = 3.43$, $P < 0.05$). The warming and vegetation-removal treatments increased soil temperatures and the warming treatment also increased air temperatures. Warming and vegetation removal synergistically increased soil temperatures (Table 1; Fig. 1e). Warming alone increased soil temperatures by 1.2°C and vegetation removal alone increased soil temperatures by 1.6°C, but together, warming and vegetation removal increased soil temperatures by 3.8°C (Fig. 1e). Air temperatures were increased 2.6°C by the warming treatment, but were unaffected by vegetation removal (Table 1; Fig. 1f).

Table 1 Summary of ANOVA for effects of warming and vegetation (*Veg*) removal on edaphic, productivity, and epifaunal response variables; *df* = 1, 28 for all models except *Spartina patens* biomass where *df* = 1, 14 because data were collected only from vegetated plots

	Warming		Veg removal		Warming × veg removal	
	F	*P*	*F*	*P*	*F*	*P*
Edaphic variables						
Salinity	1.70	0.20	7.65	**0.0099**	2.29	0.14
Redox potential	0.10	0.75	3.51	0.072	0.02	0.88
Potential evaporation	11.98	**0.0017**	5.52	**0.026**	1.87	0.18
Humidity	67.44	**<0.0001**	1.66	0.21	1.10	0.30
Soil temperature	61.67	**<0.0001**	101.09	**<0.0001**	2.12	**0.023**
Air temperature	170.52	**<0.0001**	0.57	0.46	3.86	0.06
Productivity						
S. patens	9.10	**0.0093**				
Chlorophyll a	0.01	0.93	19.56	**0.0001**	0.17	0.68
Epifaunal abundance						
Crustacea	0.29	0.59	4.82	**0.037**	3.02	0.093
Gastropoda	9.92	**0.0039**	8.65	**0.0065**	15.61	**0.0005**
Arachnida	0.01	0.94	0.46	0.50	4.79	**0.037**
Insecta	0.66	0.42	0.22	0.64	1.49	0.23

P values indicating significant effects (<0.05) are in *bold*

Vegetation removal increased salinity stress and desiccation stress, as indicated by potential evaporation (Table 1; Fig. 1a, c). Redox potential was marginally lower in vegetation-removal plots indicating greater anoxia stress, though not significantly so, due to large between-plot variation (Fig. 1b). The warming treatment, on the other hand, slightly decreased desiccation stress, as indicated by lower potential evaporation rates and higher humidity (Table 1; Fig. 1c, d). Warming had no effect on salinity or redox potential.

Ecological response

Warming increased vascular plant biomass production by 38% (Table 1; Fig. 2). Despite strong effects of warming treatments on vascular plants, however, there was no effect of warming treatment on algal productivity, indicated by chlorophyll a concentration (Fig. 3). In contrast, there was a strong effect of vegetation removal on algal productivity (Table 1; Fig. 3). Vegetation removal increased algal productivity by 133% relative to controls.

In 4 weeks of trapping epifauna, we collected over 2,000 individuals of 26 morphospecies belonging to classes Crustacea, Gastropoda, Insecta, and Arachnida (and a single juvenile fish, class Actinopterygii, excluded due to rarity). The most common animal was the amphipod *Orchestia grillus* ($n = 1{,}229$), and the pulmonate snail *Melampus bidentatus* was the second most common ($n = 118$). In MANOVA, warming and vegetation treatments had a significant interactive effect on epifaunal composition (interaction, $F_{1,24} = 5.07$, $P < 0.01$), although without vegetation removal, warming had no effect (warming effect, $F_{1,24} = 2.30$, $P = 0.0772$; vegetation-removal effect, $F_{1,24} = 2.88$, $P < 0.05$). Crustacean abundance was negatively impacted by vegetation removal (Table 1; Fig. 4). Gastropods were less abundant in all treatments relative to controls and least abundant in vegetation-removal treatments (Table 1; Fig. 4). Arachnid and insect abundances were not significantly affected by vegetation-removal or warming treatments (Table 1; Fig. 4).

Discussion

Both warming and vegetation-removal treatments had large effects on temperature. Our temperature increase manipulation was intended to cause moderate warming of 1–3°C, as is expected to occur in the northeastern US by mid-century (Frumhoff et al. 2007; IPCC 2007), and accomplished this degree of warming. Removing vegetation had more substantial effects on soil temperature than did the warming treatment (Fig. 1e), which highlights the capacity of the plant canopy to lower temperature.

Warming and vegetation treatments also affected abiotic stress levels, but in unanticipated ways. Whereas warming and vegetation-removal treatments had an interactive effect on soil temperature, this was not true of salinity, desiccation, and anoxia stresses. As expected, based on the findings

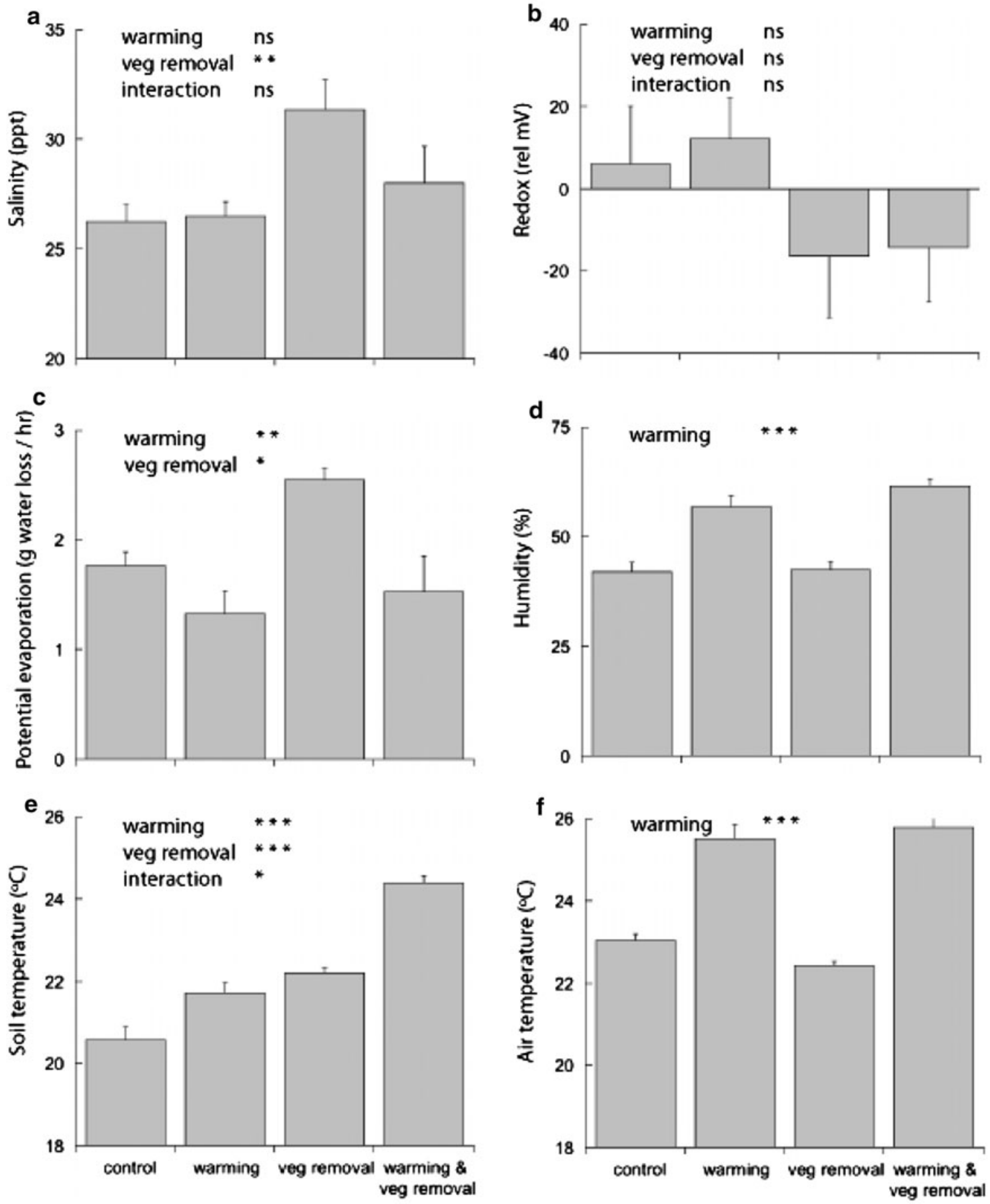


Fig. 1 The effects of warming and vegetation (*veg*)-removal treatments on **a** soil salinity, **b** redox potential, **c** evaporation, **d** humidity, **e** soil temperature, and **f** air temperature (means ± SE). See text for measurement methods. Table 1 summarizes the results of a factorial two-way ANOVA for each graph's response variable. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, *ns* no significant effect or $P > 0.05$

of other vegetation-removal experiments (Bertness 1991b; Bertness and Ewanchuk 2002; Whitcraft and Levin 2007), vegetation removal increased all abiotic stresses. The warming treatment, on the other hand, reduced desiccation stress and did not exacerbate salinity stress. Temperature and salinity stress are generally positively correlated due to the positive effects of warming on seawater evaporation, which leaves salt deposits in soils (Bertness and Ewanchuk 2002; Chapman 1974). However, in open-top warming chambers, humidity was increased and potential evaporation rate reduced (Fig. 1c, d), which decoupled thermal and salinity stresses (Fig. 1a). In part, this effect was an artifact of open-top warming chambers. However, this allowed us to somewhat isolate thermal effects, because only thermal

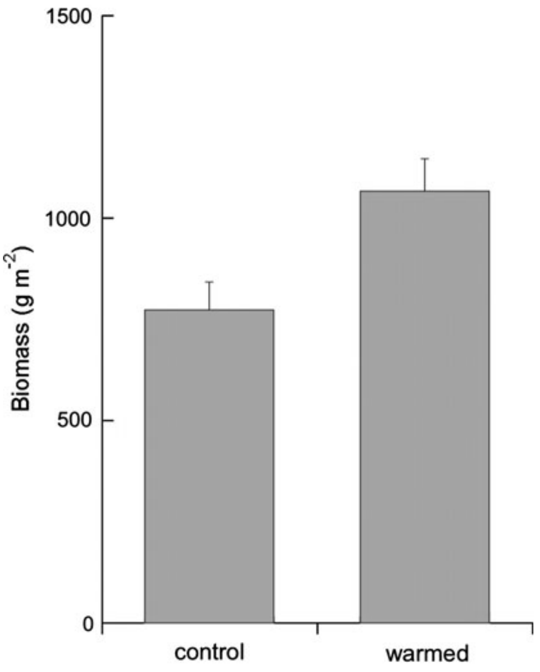


Fig. 2 Effect of warming on *Spartina patens* aboveground biomass (September 2005; mean ± SE). In a one-way ANOVA, warming had a significant effect on biomass production (Table 1)

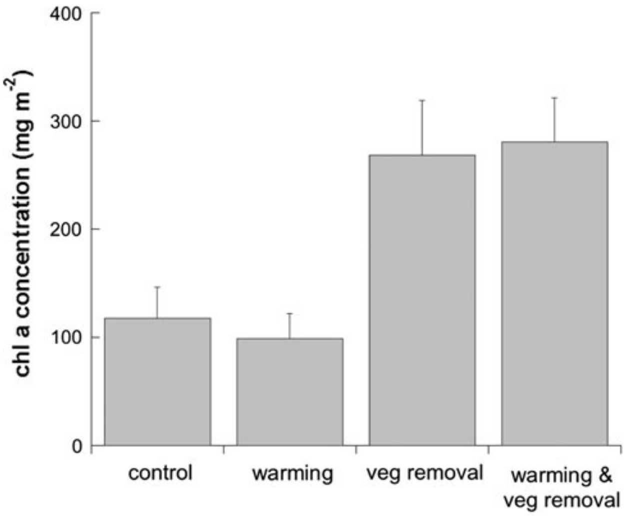


Fig. 3 Effects of warming and vegetation-removal treatments on chlorophyll a concentration (mean ± SE), sampled in August 2005, from the top 5 mm of soil cores. In a two-way factorial ANOVA, vegetation-removal treatment singularly affected chlorophyll concentration (Table 1)

stress was interactively affected by the two experimental treatments.

Warming effects in a *Spartina patens* marsh community

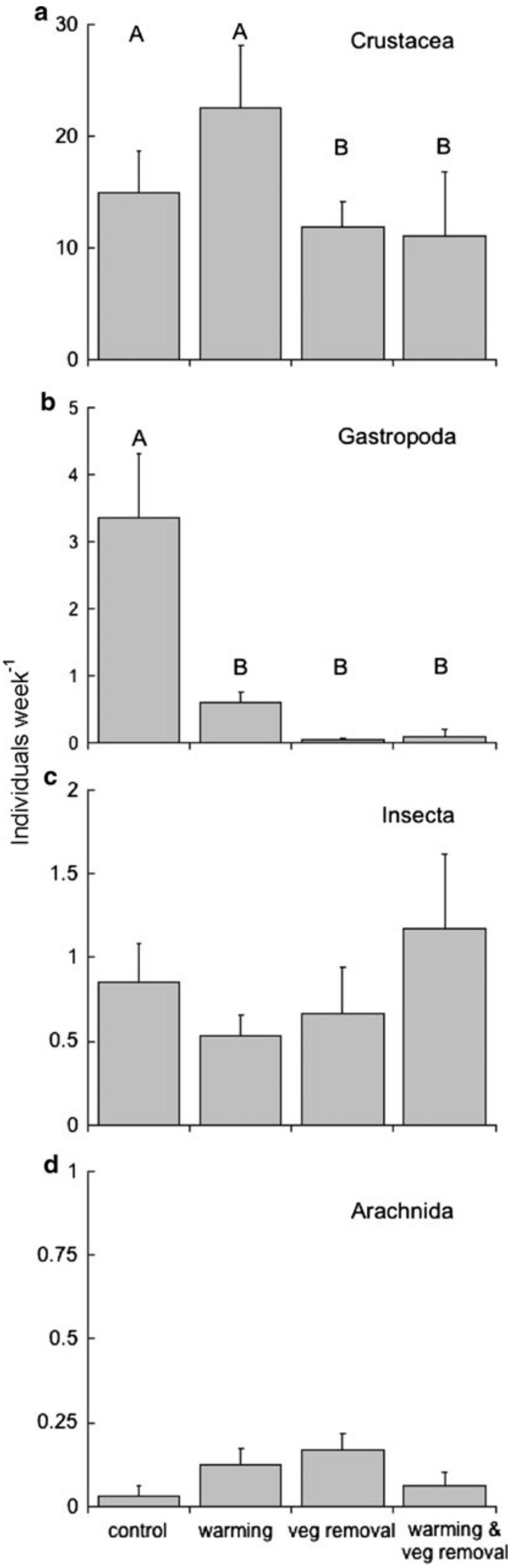
Warming did not affect the salt marsh community as expected. In contrast to the notable effects of vegetation removal, there was no consistent effect of the warming treatment alone or in combination with vegetation removal on algal production or epifaunal composition. These results suggest that thermal stress is not as substantial an environmental stress for salt marsh organisms in the New England region as salinity, desiccation, and anoxia stresses and that amelioration of thermal stress is not as important an ecological role of the foundation species *S. patens* as its effects on salinity, desiccation, and anoxia.

Temperature increase had a single strong effect in this study, from among the variety of indicators that we examined: warming increased vascular plant productivity. This is the first study to find such a result in the *S. patens* zone. In response to experimental warming, Charles and Dukes (2009) observed a productivity increase in *S. alterniflora* but not *S. patens*, perhaps because their study used a different chamber design that generated a smaller temperature effect.

Latitudinal patterns in *S. alterniflora* productivity, greater at lower latitudes, indicate that climate affects productivity at large scales (Turner 1976). The prediction from our experimental results, that higher temperatures will increase *S. patens* productivity in New England, is consistent with this latitudinal pattern and corresponds closely to an estimate of *S. alterniflora* productivity increase of 10–40% for a 2–4°C temperature increase, which was based on a regression between climate and productivity from samples spanning a latitudinal gradient (Kirwan et al. 2009).

Importance of foundation species in salt marshes

Our results reiterate the key role of foundation species in salt marshes. We found that *S. patens* regulates abiotic stresses and supports populations of amphipods and snails (Fig. 4), which are important detritivores and prey sources for predatory fish and crabs. When *S. patens* was removed, abiotic stress increased, the abundance of detritivores (e.g., the dominant Crustacean, the detritivore amphipod *Orchestia grillus*) declined, and the soil surface became algae-enriched, indicative of light limitation and/or greater grazing pressure (e.g., by the dominant Gastropod, *Melampus bidentatus*) under the plant canopy. Ludlam et al. (2002) found a similar reduction in salt marsh invertebrates after the removal of *S. patens* for salt marsh hay collection. Other studies have noted the ability of *Spartina* spp. to reduce abiotic stress and facilitate salt marsh invertebrates (Bortolus et al. 2002; Whitcraft and Levin 2007). We find that this response is likely due to amelioration of abiotic stresses other than, or in combination with, thermal stress, rather than thermal stress alone, because the warming treatment alone failed to elicit this community response.



◀ **Fig. 4** The effect of warming and vegetation-removal treatments on the abundance of epifaunal organisms: **a** Crustacea (crustaceans), **b** Gastropoda (snails), **c** Insecta (insects), and **d** Arachnida (spiders and mites). Values are the mean (±SE) value of individuals sampled per week with pit traps in June and July 2005. *Letters above bars* indicate differences between treatment combinations in Tukey's honest significant difference post hoc tests

These effects of foundation species removal on salt marsh community composition raise conservation concern for the die-off of salt marsh grasses in many parts of the western Atlantic (Bertness and Silliman 2008). In New England, large-scale die-offs of *S. alterniflora* attributed to intense herbivory by the crab *Sesarma reticulatum* have been reported recently (Holdredge et al. 2009; Smith 2009). Our results suggest that die-offs have the potential to affect salt marsh habitat quality and food webs.

Foundation species and climate change

Although we expected the importance of the foundation species to increase during simulated climate warming, we did not find strong evidence supporting this hypothesis in the New England high marsh. Instead, we found that the loss of foundation species elicited greater community change than climate warming. Our hypothesis of increased community facilitation by foundation species in response to warming may hold true in other environments, particularly ones such as deserts (Kearney et al. 2009) and the high rocky intertidal (Somero 2005) in which thermal stress is a more critical community regulator than in the salt marsh, where additional abiotic stressors of salinity, desiccation, and anoxia complicate predictions.

The New England salt marsh system may also be unique in that the foundation species *S. patens*, a C_4 grass, is more tolerant of temperature increase than the associated community of marine plants and invertebrates. In communities dominated by thermally susceptible foundation species, climate warming may negatively affect foundation species and trigger cascading effects in the associated community (Altieri et al. 2007). For example, observations of coral reef fish communities following warm spells indicate that temperature increase can trigger community shifts through adverse effects on coral foundation species (Booth and Beretta 2002), and a similar idea has been proposed for mussel beds (Smith et al. 2006).

In the case of *S. patens*-dominated New England salt marshes, however, our results suggest that global temperature increase, predicted to alter biogeochemical cycles and species composition in many ecosystems (e.g., Klein et al. 2004; Oberbauer et al. 2007; Walker et al. 2006; Zavaleta et al. 2003), may not have as large an effect as other disturbances. In particular, we predict that disturbances that result in large-scale loss of foundation species will severely affect New England salt marsh ecosystem function.

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